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Craseonycteris thonglongyai.

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Craseonycteris Hill, 1974

Craseonycteris Hill, 1974:304. Type species *Craseonycteris thonglongyai* Hill.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Craseonycteridae, Genus *Craseonycteris*. The genus *Craseonycteris* includes one living species, *Craseonycteris thonglongyai*.

Craseonycteris thonglongyai Hill, 1974

Old World Hog-nosed Bat

Craseonycteris thonglongyai Hill, 1974:305. Cave near Forestry Station, Ban Sai Yoke, Kanchanaburi, Thailand (lat. 14°26′N, long. 98°51′E).

CONTEXT AND CONTENT. Context noted above under genus *Craseonycteris*. There are no subspecies.

DIAGNOSIS. *Craseonycteris thonglongyai* may be distinguished from all other bats on the basis of its very small size; a thickened, vertical narial pad or plate; large ears, not joined; moderately long tragus, narrow and rounded at the tip, with an oblate anterior swelling about halfway along its length; distal phalanx of third digit very long (equal to subequal to third metacarpal), reflexed beneath wing; tail absent; uropatagium well developed; calcar absent. The structure of the premaxilla is unique among bats (Fig. 1); palatal branch greatly reduced and not in contact with bony palate; nasomaxillary branch long, slender, and expanded dorsally; both premaxillae fused at the dorsal and ventral midline, thus ringing the nasal aperture.

GENERAL CHARACTERS. *Craseonycteris thonglongyai* was illustrated and described in detail by Hill (1974). In addition, a general description with photographs (including one of the cave at Ban Sai Yoke) was presented by Lekagul and McNeely (1977).

Selected external measurements (in mm) of 16 to 17 males and 8 to 9 females from the original series: width of narial pad, 3.8 to 4.4; width of narial ridge, 1.9 to 2.5; length of ear, 9.0 to 10.2; width of ear, 7.3 to 8.5; length of tragus, 3.8 to 4.2; length of tibia, 11.7 to 12.9; length of foot (with claw), 5.8 to 6.8; length of forearm, 22.5 to 25.8; length of thumb, 4.6 to 5.3; length of metacarpals 2 to 5, respectively, 23.9 to 26.5, 19.7 to 21.7, 21.7 to 23.8, 21.7 to 23.7; length of proximal phalanx of digits 2 to 5, respectively, 0.40 to 0.55, 6.4 to 7.1, 3.5 to 4.3, 5.2 to 5.9; length of distal phalanx of digits 2 to 5, respectively, 0.40 to 0.63 (cartilaginous), 18.7 to 21.5, 9.7 to 10.8, 5.9 to 7.0.

Selected cranial measurements of 7 to 12 males and 4 to 5 females from the original series: greatest length of skull, 10.3 to 11.5; condylocanine length, 9.6 to 10.1; condylobasal length, 9.5 to 10.3; length of palate, 3.8 to 4.2; palatalar length, 3.6 to 3.9; width across antorbital foramina, 3.7 to 4.0; lacrimal width, 4.2 to 4.6; width across rostral swellings, 3.9 to 4.4; zygomatic breadth, 5.5 to 6.0; postorbital breadth, 2.1 to 2.3; breadth of braincase, 5.3 to 5.7; mastoid breadth, 5.7 to 6.0; height of braincase, 3.9 to 4.3; breadth across canines, 2.8 to 3.2; length maxillary toothrow (C–M3), 3.6 to 3.9; width across M3–M3, 4.5 to 4.9; post-palatal breadth, 1.4 to 1.5; width across pterygoid wings, 1.7 to 2.0; length of tympanic bulla, 2.3 to 2.7; breadth of tympanic bulla, 1.5 to 1.9; length of cochlea, 1.8 to 2.2; breadth of cochlea, 2.0 to 2.3; breadth of basioccipital, 0.5 to 0.7; length of mandibular toothrow (C–M3), 3.9 to 4.2; length of mandible, 6.7 to 7.1; length of right ramus, 6.9 to 7.3.

The small size of *C. thonglongyai* (length of head and body, 29 to 33; weight, 1.7 to 2.0 g; fide Wood, 1976) makes it the smallest living mammal or, at least, among the smallest mammals which include: Asian pygmy shrew (*Suncus etruscus*: head and body length, 36.0 to 52.0; weight, 1.5 to 2.5 g); American pygmy shrew (*Microsorex hoyi*: head and body length 58.0 to 78.0; weight, 2.2 to 3.8 g); lesser club-footed bat (*Tylonycteris pachypus*: head and body length, 34.0 to 40.0; weight, 3.5 to 5.0); and West African tiny pipistrelle (*Pipistrellus nanulus*: head and body length, 38.0, weight 2.5 g). There is some overlap in forearm length with *Craseonycteris* and those bat species listed above as well as several other tiny species such as *Rhogeessa parvula*.

DISTRIBUTION. The species is known so far only from the limestone caves at the type locality in west-central Thailand (Fig. 2). In view of the fact that the geographic distributions of many species of the cavernicolous bat fauna of southeastern Asia currently are not well-defined, future field investigations will probably result in a somewhat more extensive geographic range for *C. thonglongyai*.

FORM AND FUNCTION. *Craseonycteris thonglongyai* has a number of anatomical features worthy of further comment. As noted above, the muzzle, with its lateral swellings and flat, fleshy vertical narial pad, is rather "suiform" in appearance; hence the common name "hog-nosed" bat. The nostrils are crescentic with a shallow groove extending dorso-laterally from their

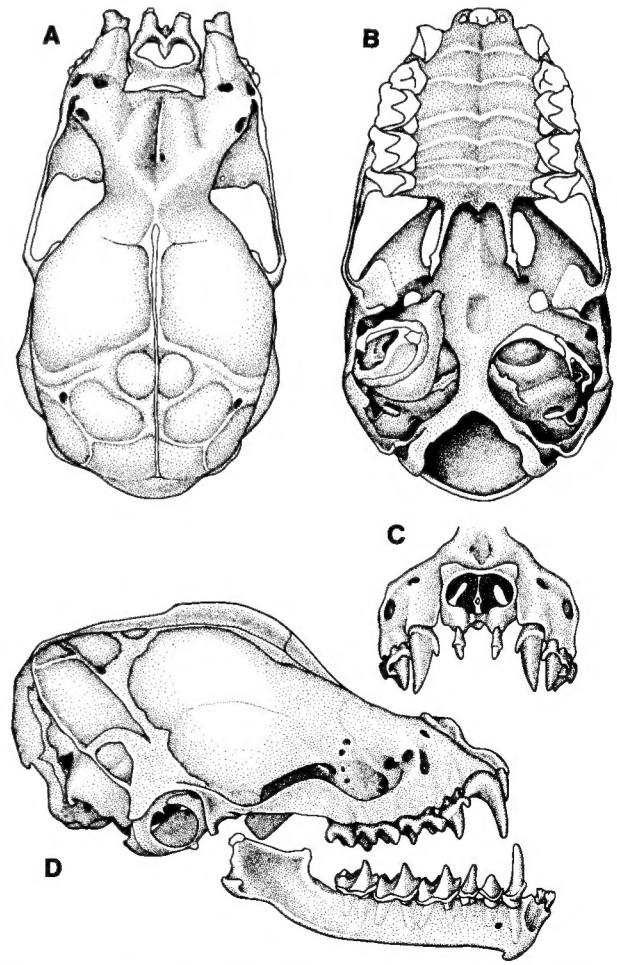

FIGURE 1. Skull of *Craseonycteris thonglongyai*. A, Dorsal view; B, Ventral view, with soft palate; C, Anterior view premaxillae and rostrum; D, Lateral view cranium and lower jaw. All drawn from SMF No. 54515 (adult male).

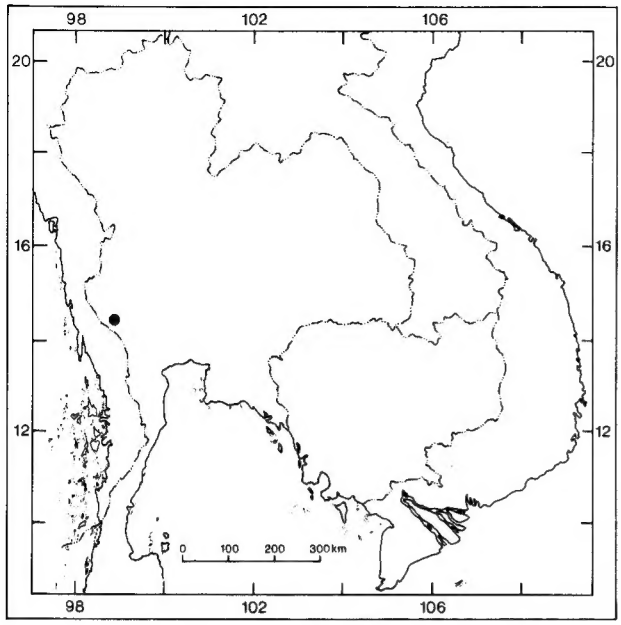

FIGURE 2. Map showing the distribution of *Craseonycteris thonglongyai* in southeast Asia.

upper margins; these grooves divide the narial plate into lateral and medial elements. The narial pad and medial portion of the lower lip are naked, for the most part, but the edges of the lateral swellings of the muzzle and chin are clothed with short, stiff vibrissae. The narial pad is generally similar to that of rhinopomatids, although the external nares of *Rhinopoma* are valvular, less inclined vertically, and not separated by a well-developed internarial septum.

The eyes are extremely small and concealed by the facial hair. The ears are large and membranous. The tragus also is long (nearly 50% of the length of the ear) and well developed. It is narrow and constricted at the base, broadened in the mid-portion with tiny, lateral serrations, and narrow and lanceolate distally with a blunt, rounded tip. There is a marked oblate swelling on the antero-medial edge of the mid-portion of the tragus; antitragus is weakly developed. Males possess a rounded, glandular swelling on the lower portion of the throat; this gland is less prominent or absent in females. Females possess a pair of pectoral mammae and a pair of closely associated, inguinal false teats located just above the genital plate; this latter feature, which is probably primitive, also is found in the Rhinopomatidae, Rhinolophidae, Hipposideridae, Megadermatidae, Nycteridae, and has been reported from the Nyctophilinae in the Vespertilionidae.

The tail and calcars are absent. The uropatagium is well developed, narrow proximally and broadened distally; it terminates medially slightly beyond the middle of the tibia, and is inserted 3 to 4 mm above the ankle. The foot is long and slender, phalangeal formula (pes) 2-3-3-3-3, and the toes are subequal in length.

The dorsal pelage is long, lax, and greyish brown; ventrally the pelage is somewhat shorter and paler (from specimens preserved in alcohol). Lekagul and McNeely (1977) reported specimens with brown to reddish brown dorsal pelage which they attributed to "color phase" variation.

The structure of the wing of *Craseonycteris thonglongyai* was discussed in great detail by Hill (1974) and later by Smith and Starrett (1979) in an extensive morphometric analysis of chiropteran wings. The propatagium is broad and attaches to the distal end of the metacarpal of the thumb which is rather short and has a strong claw. The second digit consists of a long metacarpal, a short, bony proximal phalanx which is usually fused to the metacarpal, and terminates with a short, tapered cartilage. The structure of digit 3 is unique among bats. Metacarpal 3 is relatively short (43.4% of the digital length) compared to 4 and 5 (61.5 and 65.6% of the digital length, respectively) which are somewhat longer and approximately equal in length (Smith and Starrett, 1979). The proximal phalanx of digit 3 is markedly short. The most striking feature of digit 3 is the extremely long distal phalanx (42.2% of the digital length) which nearly equals the length of the metacarpal (Smith and Starrett, 1979). This phalangeal element is curiously bowed and shares a broad, highly mobile joint with phalanx 1; it is reflexed beneath the wing in its resting posture. Digit 4 consists of a relatively long metacarpal, noted above, a short proximal phalanx, and a relatively long distal phalanx (nearly 50% of the length of the metacarpal) which is partially reflexed beneath the wing when at rest. Metacarpal 5 also is relatively long and the two phalangeal elements are nearly equal in length; the distalmost is slightly the longer. Smith and Starrett (1979) computed the tip index (1.86) and an overall aspect ratio (5.64) for *C. thonglongyai* which are slightly above and slightly below the respective averages for these ratios for all bats (tip index, 1.85 and overall aspect ratio, 5.86). Prompted by comments made by Findley et al. (1972) concerning an average or below average aspect ratio coupled with a high tip index, Hill (1974) suggested a hovering or, at least, a partial hovering ability for *C. thonglongyai*. Smith and Starrett (1979) agreed, but their supposition was founded more on the structural nature of digit 3, with its long and apparently highly mobile distal phalanx, than on any relationship between tip indices and aspect ratios. Generally, the wing of *Craseonycteris* shares many features with those of the Nycteridae, Megadermatidae, Rhinolophidae, and Hipposideridae.

Aside from the unique structure of the premaxillae, noted above, the cranium of *C. thonglongyai* presents some other noteworthy features. The skull is very small with a globose braincase and a prominent sagittal crest that is pronounced anteriorly over the frontal bones (Fig. 1A, D); usually the crest slopes gently to a point immediately above the narrowest postorbital region, but occasionally it terminates abruptly (dotted line, Fig. 1D) slightly posterior to this point. Lambdoid crest is obsolete. The parietals are inflated and these suggest the morphology of the underlying hindbrain. The inferior colliculi appear to be large as is usual for Microchiroptera (Henson, 1970). However, the superior colliculi also appear to be large and well developed, a feature shared with, at least, *Saccopteryx* and, to a lesser extent, *Hipposideros* (Henson, 1970). Anteriorly, the rostrum is broad due to the marked inflation of the maxillary and nasal sinuses; there is a moderate rostral depression. Several foramina pierce the anterior portion of the inflated maxillary (Fig. 1A, C, D); these presumably conduct vascular and neural trunks to the specialized narial pad. Neither postorbital processes nor supraorbital ridges are present. The zygoma are slender, moderately expanded dorsally in the malar region, extremely narrow at the temporal root, and not flared laterally (Fig. 1A, D).

The bony palate is short, wide, and has a deep and broadly U-shaped anterior emargination (Fig. 3B). Posteriorly, the bony palate terminates abruptly behind last upper molars (Fig. 3B); a bony post-palatal extension is absent. The soft palate has six transverse ridges; the first five have a small medial notch (Fig. 1B). There is a small and shallow, dimple-like medial depression in the basisphenoid (Fig. 1B). The tympanic bullae are large, flattened on the medial margin, and have a prominent styliform process; *processus furcatus bullae* (Henson, 1970) reduced (Fig. 1D).

The lower jaw is slender and delicately built. The chin region, below the incisors, is curiously sculptured (Fig. 3C) and the mandibular symphysis is deep and has a prominent ventral flange (Fig. 1D). The coronoid process is extremely low and moderately flared laterally; anterior portion equal or slightly below level of articular facet (Fig. 1D). The structure of the angular process is distinct and rather peculiar among bats; not only does it have many flanges and ridges, but it is flared laterally (at an acute 90° angle) approximately twice the width of the articular condyle (Fig. 3A). This morphology, coupled with the anterior prominence of the sagittal crest, affects the efficiency of the large, anterior branch of the temporalis muscle and thus concentrates its force on the molar arcade. The malar flange on the zygoma also may contribute to this masticatory apparatus by providing a larger area of origin for the masseteric muscle.

Dental formula is i 1/2, c 1/1, p 1/2, m 3/3, total 38. The upper incisors are relatively large, widely separated from canines, acutely triangular from the front, and have a strong basal cingulum (Fig. 1C). The lower incisors are tricuspid, not imbricated, lack a basal cingulum and posterior supporting cusp, and the tiny cusps are slightly recurved (Figs. 3A, C). The upper canines are long and slender with a prominent antero-lingual, cingular cusp (Figs. 1C, 3B); lower canines somewhat longer and more slender than uppers (Figs. 1D, 3A, C). The upper premolars (P4; dental notation after Miller, 1907) large with prominent anterior cingular cusp and strong posterior blade (Figs. 1D, 3B). First lower premolar (p2) is subtriangular with moderately high central cusp (Figs. 1D, 3A); cingulum is strong on all lower teeth, except in-

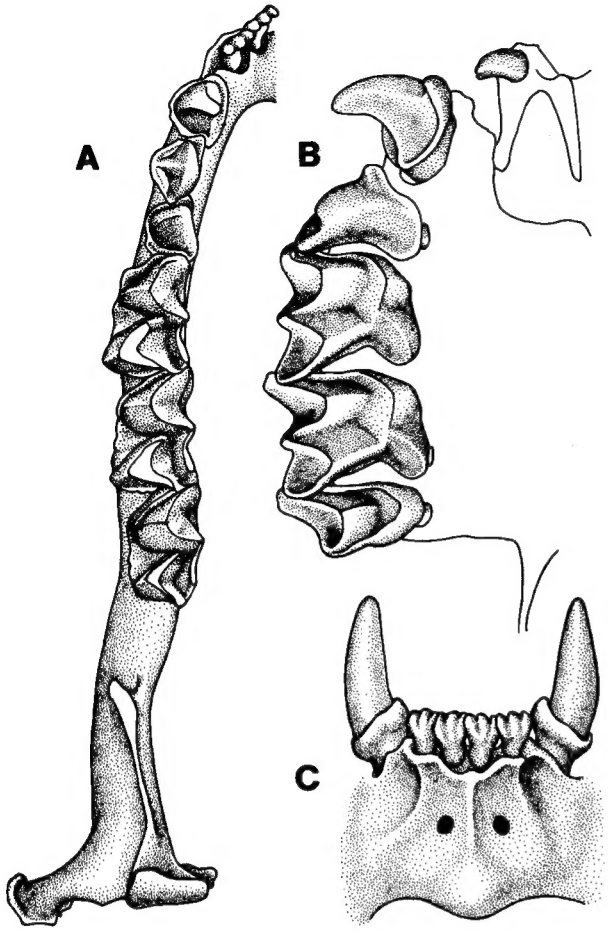

FIGURE 3. Dentition of *Craseonycteris thonglongyai*. A, Left lower dentition and lower jaw; B, Right upper dentition, premaxillae, and bony palate; C, Anterior view of lower incisors and chin. All drawn from SMF 54515 (adult male).

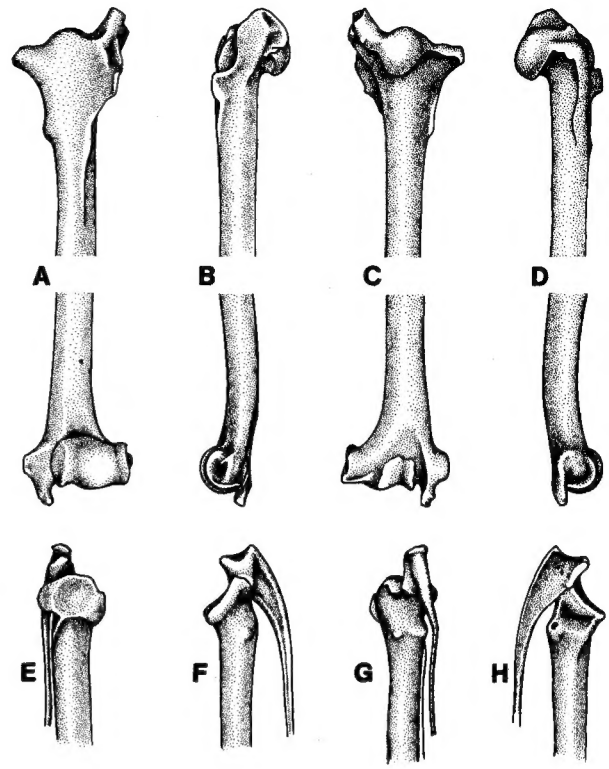

FIGURE 4. Humerus (A–D) and proximal end of radius and ulna (E–H) of *Craseonycteris thonglongyai*. A, E, Anterior view; B, F, Dorsal view; C, G, Posterior view; D, H, Ventral view of respective wing bones. All drawn from SMF 54515 (adult male).

cisors. The second lower premolar (p4) is short, antero-posteriorly, and with an unusually long and slender (caniform) central cusp (Figs. 1D, 3A). The first two upper molars (M1 and M2) have the typical chiropteran W-shaped ectoloph; protocone is low and broadly rounded; hypoconal shelf lobate and acutely sloped below protoconal platform; distinct hypocone absent (Fig. 3B). Coronal morphology of last upper molar (M3) is reduced; pre- and post-metacristae and metacone are absent (Fig. 3B). First two lower molars (m1 and m2) have well-developed trigonid and talonid, equal to subequal in size; trigonid is slightly higher than talonid (Figs. 1D, 3A). Talonid of last lower molar (m3) is distinctly smaller than trigonid (Fig. 3A). On all lower molars the entocristid (connects metaconid and entoconid) is strong and the postentocristid (connects entocristid to hypoconulid) absent; hypoconulid obsolete (Fig. 3A).

Hill (1974) discussed and illustrated many aspects of the post-cranial skeleton. The scapula is narrow, infraspinous fossa quite strongly faceted, acromion process weak, and the coracoid is flared laterally. The proximal end of the humerus is distinctive in that it is more highly sculptured with ridges and flanges than that of any other chiropterans. The greater tuberosity (trochiter) is large and extends well beyond the rather small and rounded head of the humerus. The long trochiter probably affects a locking mechanism as suggested by Smith (1972); articular facet on medial face absent (Fig. 4A–D). Hill (1974) noted the apparent absence of a median anterior pectoral crest that is usually present as a low to high blade in other bats. As indicated by this author, in *Craseonycteris thonglongyai* the pectoral crest is indeed present, but markedly modified; it is laid flat along the dorsal margin against the trochiter (Fig. 4A–C). The lesser tuberosity (trochin) also is large and supported by a strong flange which extends distally along the shaft. Distally, the spool-shaped articular facet (capitellum, trochlea, and epitrochlea) is displaced off the central axis of the shaft (Fig. 4A). The capitellum is globose and the trochlea and epitrochlea are narrow; these articular facets extend onto the ventral portion of the distal end of the humerus (Fig. 4C). There is a strong distal spinous process that extends well beyond the distal articular surfaces. The proximal articular facets of the radius reflect the size and shape of the distal articular surfaces of the humerus (Fig. 4E–H). The radial ridge is strong, short, and acutely angled toward the ventral margin; flexor fossa is small. The ulna is a prominent feature of the elbow joint, but its thin shaft is unusually bent so that it lies along the ventral margin of the radius (Fig. 4E, G); normally, it extends along the posterior face of the radius. There are two prominent tuberosities on the posterior surface of the proximal end of the radius (Fig. 4G) which are probably usually involved with an enlarged head(s) of the extensor carpi ulnaris.

The lower three thoracic vertebrae, lumber vertebrae (except last two), and sacral vertebrae are fused. The pelvis is small, delicately built, acicular or pubic spine absent; and ischium has a thin, delicate ascending ramus. The femur is slender and weak; proximally the trochanters are relatively small, the lesser slightly the larger, medial ridge well developed and flange-like, and there is no proximal deflection. The fibula is thread-like, tapered, and about 50% of the length of the tibia.

ONTOGENY AND REPRODUCTION. As yet, nothing is known of the reproduction and development in this species.

ECOLOGY AND BEHAVIOR. *Craseonycteris thonglongyai* has been collected or observed at Ban Sai Yoke on five separate occasions over a span of several years beginning in October 1973 (Lekagul and McNeely, 1977). They suggested that this little bat was a permanent resident in these caves, although data for the rainy season are lacking. The Ban Sai Yoke region is riddled with many limestone caves, some quite extensive, however, Lekagul and McNeely (1977) noted that relatively few of these are inhabited by bats or have bat droppings. They noted that bat habitation or sign thereof may be obscured by seasonal flooding. In addition, they indicated that the forest around Ban Sai Yoke has been totally cleared which may explain the paucity of bat habitation and/or activity in and around these caves. Lekagul and

McNeely (1977) did not indicate other bat species (if any) that also inhabit the caves at Ban Sai Yoke. The individuals of *C. thonglongyai* which have been captured or observed were found in small caves, far from the entrance in the most remote caverns, hanging high on the ceiling and well separated from each other. They are apparently very wary, as 10 to 15 individuals seen in a roost, on one occasion, took flight immediately upon being disturbed. Lekagul and McNeely (1977) reported seeing *Craseonycteris* flying around the tops of bamboo clumps and teak trees on two separate occasions: apparently, they emerge just at dusk. They suggested that *C. thonglongyai* is a foliage gleaner (a possibility first considered by Hill [1974] from the structure of the premaxillae) and, perhaps, also captures small insects on the wing.

The food habits of *Craseonycteris* have not been recorded. J. D. Smith (pers. comm.) reported examining the stomach contents of an adult male (Senckenberg Museum 54515) from among those originally collected. The stomach of this individual contained body fragments of small beetles (5 to 6 mm size range); lygaeid (?) hemipterans (5 to 7 mm size range); small Hymenoptera; an orthopteran (10 to 12 mm size range); homopteran wing fragments; and chelicera and legs of a spider. These prey items would seem to corroborate the hypothesized aerial and foliage gleaning foraging behavior of the species proposed by Hill (1974) and Lekagul and McNeely (1977). In a commentary regarding food habits of bats and supposed dietary competition, Van Valen (1979) noted that at least eight families of bats (presumably insectivores), "seem to partition a generally similar array of food in ways that need to be discovered in detail." He cited the ground-foraging of rhinolophoids and, "the narrow distribution of the bumblebee-sized" Craseonycteridae as partial exceptions. His intention does not seem clear, but we believe it is premature to propose such ecological generalities on the basis of the rather sketchy distributional and biological knowledge of *Craseonycteris*.

Echolocation sounds of *C. thonglongyai* are of high intensity, with a constant frequency for up to 2 ms followed by a shallow downsweep of about 1 ms. The fundamental frequency is 35 kHz, the second harmonic at 70 kHz rather stronger, and there is a weak third harmonic at 105 kHz, all producing characteristic "tweets" on a tuned bat detector (Pye, pers. comm.).

Hard ticks (family Ixodidae) and chigger mites (family Trombiculidae) have been reported from *C. thonglongyai* (Lekagul and McNeely, 1977).

REMARKS. The phylogenetic relationships of *Craseonycteris thonglongyai* are of considerable interest. The species constitutes the sole known representative of the family Craseonycteridae, proposed concurrently by Hill (1974), and resembles the Rhinopomatidae in some features of the nose, leading edge of the wing, absence of the calcars, inflated nasals and maxillaries, free premaxillae, and many aspects of the dentition. It differs from this family notably by the unspecialized nature of the nostrils, large unconnected ears, specialized tragus, modified and uniquely structured wing, absence of the tail, and structure of the scapula, humerus, radius, and pelvis. *Craseonycteris* resembles bats of the family Emballonuridae (also associated with rhinopomatids) by the structure of the nostrils and the presence of rostral swellings; to a limited extent the structure of the premaxillae is similar. The structure of the tragus, lack of a tail, absence of postorbital processes and elaborate basioccipital pits, the dentition, and organization of the shoulder joint distinguish *Craseonycteris thonglongyai* from emballonurids. In general terms, and especially in the structure of the skull and dentition, *Craseonycteris* appears to share a closer relationship with the Rhinopomatidae than with the Emballonuridae. Smith (1976) implied a closer affinity to the latter and Van Valen (1979) suggested, tentatively, that *Craseonycteris* might be a descendant of a primitive emballonurid ancestor. Hill (1974) considered the Craseonycteridae to have resulted from a dichotomy of the rhinopomatid/emballonurid stock, sharing some features of both and considerably derived in other features such as structure of the cranium, dentition, and wing.

Craseonycteris thonglongyai has been variously referred to as the Old World hog-nosed bat, hog-nosed bat, or Kitti's hog-nosed bat (all allusions to the suiform muzzle); and/or butterfly bat or bumblebee bat (all allusions to its small size and delicate appearance). It was named in honor of Kitti Thonglongya, the Thai mammalogist who discovered it and whose untimely death in 1974 occurred before it could be described.

According to Article 29 of the International Code of Zoological Nomenclature the family should be known as the Craseonycteridae, the correct formation of its name. However, the family name for the slit-faced or hollow-faced bats, genus *Nycteris* Cuvier and Geoffroy, 1795 is generally accepted as Nycteridae and has been for many years. Article 29 (d) states that a family name proposed before 1961 but based upon an incorrectly formed stem is not to be amended if it is in general use, while incorrectly formed family names published after 1960 are to be corrected wherever they are found. To avoid confusion and in the interests of consistency the formation Craseonycteridae was adopted in the original account and is used again here. Similar arguments affect the Archaeonycteridae Revilliod, 1917, and Icaronycteridae Jepsen, 1966.

There are specimens of *Craseonycteris thonglongyai* in the Thai National Reference Collections, Bangkok; the British Museum (Natural History), London; Natur-Museum Senckenberg, Forschungsinstitut Senckenberg, Frankfurt am Main; and Loma Linda World Museum of Natural History, Loma Linda Univ., Riverside, California. The species and the caves at Ban Sai Yoke have been filmed by the British Broadcasting Corporation.

Randall T. Schuh, American Museum of Natural History, assisted in the identification of stomach contents.

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